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A new species of genus *Tylototriton* (Caudata, Salamandridae) from northeastern Guangxi, China

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Abstract

Currently, the genus *Tylototriton* comprises 44 species, of which 24 occur in China, and only one is formally recorded in Guangxi, China. In this study, based on evidence from molecular and morphological comparisons, we describe a new species of the genus *Tylototriton*, *Tylototriton guilinensis* **sp. nov.**, from Quanzhou County, Guilin City, Guangxi Zhuang Autonomous Region, China. Phylogenetic analysis based on mitochondrial 16S rRNA and ND2 genes strongly supported that this new species belongs to the *T. asperrimus* species group and is sister to the clade of *T. dabienicus* and *T. gaowangjienensis*. This new taxon can be distinguished from all other known congeners by the following morphological characteristics: (1) medium body size (117.86 ± 9.46 mm); (2) rib nodules flattened, indistinct, not separated, and almost in continuous longitudinal rows, forming a dorsolateral fold; (3) orange coloration of the rib nodules absent; (4) orange markings on the parotoid absent; (5) head wider than long (HDL/HDW = 0.92–0.99); (6) finger tips extending beyond the snout when forelimbs are stretched forward; (7) tips of forelimbs and hindlimbs reaching and overlapping when folded towards the body; (8) snout truncate, nearly square-shaped in dorsal view; (9) gular fold present; (10) adult males possessing cloacal papillae within the fissure; (11) peripheral area of cloaca orange; (12) the orange coloration at the ventral edge of the tail contacting the orange coloration around the cloaca. In addition, we find that *T. asperrimus* from Baise, Guangxi, actually belongs to *T. sini*.

Key Words

morphology, phylogeny, taxonomy, *Tylototriton asperrimus*, *Tylototriton guilinensis* sp. nov.

Introduction

The genus *Tylototriton* Anderson, 1871 represents a basal lineage within Salamandridae, forming a sister clade to the genus *Echinotriton* (Phimmachak et al. 2015). This genus was established in 1871 based on *T. verrucosus* Anderson, 1871, collected from Longchuan County, Yunnan Province, China (Anderson 1871). It is characterized by the presence of dorsal granules, dorsolateral bony ridges on the head, knob-like warts on the dorsolateral body, and the absence of a quadrate spine (Fei et al. 2006; Li et al. 2026). It is the most species-rich and most widely distributed genus in the family Salamandridae, primarily concentrated in southeastern and eastern Asia, spanning from the southern foothills of the Himalayas to the Indochina Peninsula, as well as in southern China (Frost

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2026). Currently, the genus *Tylototriton* comprises 44 validly recognized species (Frost 2026), of which 24 species have been documented in China to date (AmphibiaChina 2026; Frost 2026), namely: *T. anhuiensis* Qian, Sun, Li, Guo, Pan, Kang, Wang, Jiang, Wu & Zhang, 2017, *T. asperrimus* Unterstein, 1930, *T. broadoridgus* Shen, Jiang & Mo, 2012, *T. dabienicus* Chen, Wang & Tao, 2010, *T. daloushanensis* Zhou, Xiao & Luo, 2022, *T. gaowangjienensis* Huang, Xiang, Zhang, Wu & Jiang, 2024, *T. hainanensis* Fei, Ye & Yang, 1984, *T. joe* Rao, Zeng, Zhu & Ma, 2022 "2020," *T. kweichowensis* Fang & Chang, 1932, *T. liuyangensis* Yang, Jiang, Shen & Fei, 2014, *T. lizhenchangi* Hou, Zhang, Jiang, Li & Lu, 2012, *T. maolanensis* Li, Wei, Cheng, Zhang & Wang, 2020, *T. panwaensis* Grismer, Wood, Quah, Thura, Espinoza & Murdoch, 2019, *T. pseudoverrucosus* Hou, Gu, Zhang, Zeng & Lu, 2012, *T. pulcherrimus* Hou, Zhang, Li & Lu, 2012, *T. shanjing* Nussbaum, Brodie & Yang, 1995, *T. sini* Lyu, Wang, Zeng, Zhou, Qi, Wan & Wang, 2021, *T. taliangensis* Liu, 1950, *T. tongziensis* Li, Liu, Shi, Wei & Wang, 2022, *T. verrucosus* Anderson, 1871, *T. wenxianensis* Fei, Ye & Yang, 1984, *T. wufengensis* Li, Liu & Gong, 2026, *T. yangi* Hou, Zhang, Zhou, Li & Lu, 2012, and *T. ziegleri* Nishikawa, Matsui & Nguyen, 2013.

The classification within the genus *Tylototriton* has remained controversial for decades, and primarily three nomenclatures (*Yaotriton* Dubois & Raffaëlli, 2009, *Qiantriton* Fei, Ye & Jiang, 2012, and *Liangshantriton* Fei, Ye & Jiang, 2012) have been proposed to accommodate its different species. Dubois and Raffaëlli (2009) coined *Yaotriton* as a subgenus of *Tylototriton*. Subsequently, Fei et al. (2012) treated *Yaotriton* as an independent genus and coined two new taxa: *Liangshantriton* (a genus accommodating *T. taliangensis*) and *Qiantriton* (a subgenus of *Tylototriton*). Dubois et al. (2021) also treated *Yaotriton* as an independent genus. However, Poyarkov et al. (2021) rejected the use of genus *Liangshantriton* and subgenus *Qiantriton*, while they treated *Yaotriton* as a subgenus of *Tylototriton* and further partitioned the genus *Tylototriton* into five species groups. However, although the two subgenera *Tylototriton* and *Yaotriton* are phylogenetically distinct, the morphological characteristics defining these two subgenera remain unclear (Nishikawa et al. 2013a), and the morphological differences among some of the five groups are also unclear (Lyu et al. 2021). Therefore, after a comprehensive morphological review, Lyu et al. (2021) rejected the use of subgenera and reclassified the genus *Tylototriton* into three species groups based on morphological disparities and phylogenetic relationships: the *T. taliangensis* group, the *T. asperrimus* group, and the *T. verrucosus* group.

Tylototriton asperrimus was originally described based on specimens collected from Mt. Dayao, Jinxiu County, Guangxi Zhuang Autonomous Region, China. It was long considered to be widely distributed across southern China (Guangdong, Guangxi, and Guizhou) and Vietnam (Mo et al. 2014). However, recent integrated taxonomic approaches combining morphology and molecular data have revealed that populations identified as *T. asperrimus* actually represent a species complex comprising multiple paraphyletic lineages (Yuan et al. 2011; Wang et al. 2018), and several cryptic species have been identified in previous studies, such as *T. maolanensis* from Maolan, Guizhou (Li et al. 2020), *T. pasmansi* Bernardes, Le, Nguyen, Pham, Pham, Nguyen & Ziegler, 2020 from northern Vietnam (Bernardes et al. 2020), *T. sini* from Guangdong Province (Lyu et al. 2021), *T. sparreboomi* Bernardes, Le, Nguyen, Pham, Pham, Nguyen & Ziegler, 2020 from northern Vietnam (Bernardes et al. 2020), and *T. ziegleri* from northern Vietnam (Nishikawa et al. 2013b), implying that *T. asperrimus* is probably only restricted to Guangxi, China.

Currently, *T. asperrimus* is the only formally recorded species of the genus *Tylototriton* in Guangxi (AmphibiaChina 2026), with a broad distribution spanning the northern, central, eastern, and southwestern regions of the province (Mo et al. 2014; Raffaëlli 2022). However, updated surveys are needed to clarify Guangxi's *Tylototriton* diversity, as cryptic lineages and potential new species may be involved (Hernandez 2018). During recent field surveys in northeastern Guangxi, China, we collected six specimens that were initially identified as *T. asperrimus*. Subsequent morphological comparisons and phylogenetic analyses confirmed that these specimens represent an undescribed species of the genus *Tylototriton*, suggesting that species diversity of this genus in Guangxi is underestimated.

Materials and methods

Sampling

This study was carried out in accordance with the ethical guidelines issued by the Ethics Committee of Guangxi Normal University. On 11 May and 16 July 2025, a total of six *Tylototriton* specimens were collected at Tianhu Lake, Quanzhou County, Guilin City, Guangxi Zhuang Autonomous Region, China (Fig. 1). All specimens were photographed, euthanized, and subsequently preserved in 75% ethanol solution. Liver tissue samples were preserved in 99% ethanol solution. Voucher specimens were deposited at Guangxi Normal University (GXNU).

Molecular phylogenetic analyses

Genomic DNA was extracted from liver tissue samples digested with proteinase K using the standard phenol–chloroform method (Russell and Sambrook 2001). A partial fragment of the mitochondrial ND2 gene was amplified and sequenced using primers L4437b/H5934 (Matsui and Panha 2006), and a partial fragment of the 16S rRNA gene was amplified and sequenced using primers L2188 (Matsui et al. 2006)/16H1 (Hedges 1994). PCR reactions were performed in a total volume of 25 μL. The

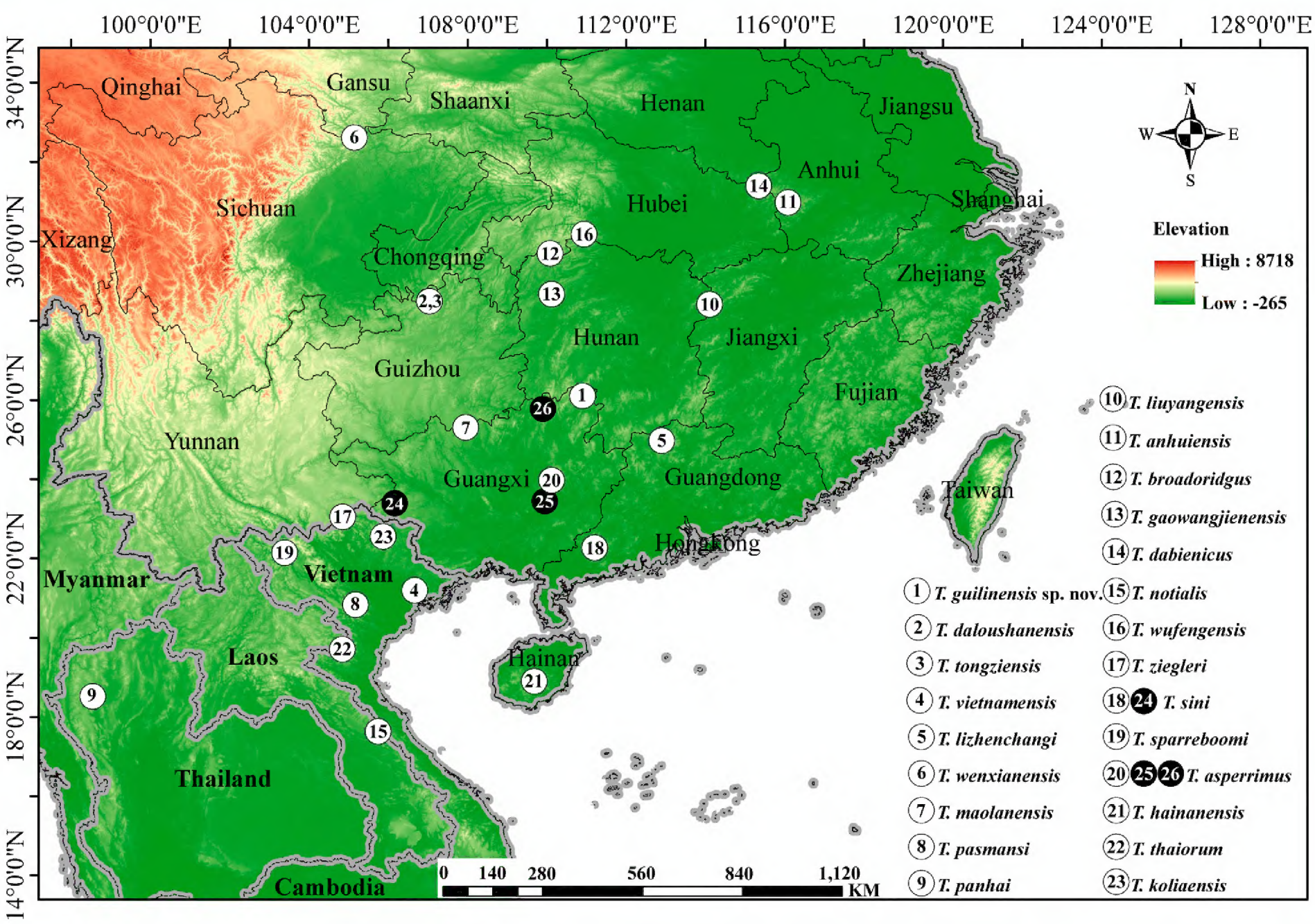

Figure 1. Map showing the distribution of *Tylototriton* species in Guangxi and the type locality (labeled with white circles) of species of the *T. asperrimus* group. 1: Quanzhou, Guilin, Guangxi, China (the type locality of *Tylototriton guilinensis* sp. nov.); 2: Suiyang, Guizhou, China; 3: Tongzi, Guizhou, China; 4: Luc Nam, Bac Giang, Vietnam; 5: Mt. Mang, Hunan, China; 6: Wenxian, Gansu, China; 7: Libo, Guizhou, China; 8: Da Bac, Hoa Binh, Vietnam; 9: Loei, Thailand; 10: Liuyang, Hunan, China; 11: Yuexi, Anhui, China; 12: Sangzhi, Hunan, China; 13: Guzhang, Hunan, China; 14: Shangcheng, Henan, China; 15: Boualapha, Khammouan, Laos; 16: Wufeng, Hubei, China; 17: Quan Ba, Ha Giang, Vietnam; 18: Mt. Yunkai, Guangdong, China; 19: Sin Ho, Lai Chau, Vietnam; 20: Jinxiu, Guangxi, China; 21: Hainan, China; 22: Que Phong, Nghe An, Vietnam; 23: Nguyen Binh, Cao Bang, Vietnam; 24: Baise, Guangxi, China; 25: Guiping, Guangxi, China; 26: Longsheng, Guangxi, China (Figure by Xiangjian Wu). The map was produced using ArcMap v.10.8.1.

PCR conditions for ND2 are as follows: initial denaturation at 94 °C for 1 min; 35 cycles of denaturation at 94 °C for 50 s, annealing at 59 °C for 50 s, and extension at 72 °C for 1 min; followed by a final extension at 72 °C for 5 min. The PCR conditions for 16S rRNA are as follows: initial denaturation at 95 °C for 4 min; 35 cycles of denaturation at 90 °C for 1 min, annealing at 61 °C for 1 min, and extension at 72 °C for 1 min; with a final extension at 72 °C for 10 min. PCR products were purified and then sequenced using the corresponding PCR primers. All new sequences have been deposited in GenBank under accession Nos. PZ247720–PZ247726 and PZ255432–PZ255438 (Table 1).

Homologous sequences of known *Tylototriton* species were downloaded from GenBank (Table 1). We selected *Echinotriton andersoni* (Boulenger, 1892) and *Echinotriton chinhaiensis* (Chang, 1932) as outgroup taxa according to Lyu et al. (2021), and sequences of them were also retrieved from GenBank. Sequences were aligned using MEGA v.12 (Kumar et al. 2024), and interspecific genetic distances were calculated under the Kimura 2-parameter (K2P) model. We used the PartitionFinder 2 module (Lanfear et al. 2017) in PhyloSuite v.1.2.3 (Zhang et al. 2020) to select the optimal nucleotide substitution models based on the Bayesian Information Criterion (BIC; Kalyaanamoorthy et al. 2017), resulting in HKY+I+G for 16S and GTR+I+G for ND2. Maximum likelihood (ML) tree inference was performed using IQ-TREE v.2.2.0 (Nguyen et al. 2015), running 5,000 ultrafast bootstrap replicates (Minh et al. 2013) under the edge-linked partition model. In addition, Bayesian inference (BI) analysis was conducted using MrBayes v.3.2.7a (Ronquist et al. 2012). Two independent searches were initiated with random starting trees, each employing four Markov chains under default heating parameters. The chains were run for 5,000,000 generations and sampled trees every 1,000 generations. The first 25% of sampled trees were discarded as burn-in, and the remaining trees were used to construct a majority-rule consensus tree and estimate Bayesian posterior probabilities.

Table 1. Species used for phylogenetic analyses in this study (T = *Tylototriton*).

No.	Species	Voucher number	Locality	GenBank accession no.	
				16S rRNA	ND2
1	*T. guilinensis* sp. nov.	GXNU YU000981	Tianhu Lake, Quanzhou County, Guilin City, Guangxi, China	PZ255433	PZ247721
2	*T. guilinensis* sp. nov.	GXNU YU000982	Tianhu Lake, Quanzhou County, Guilin City, Guangxi, China	PZ255434	PZ247722
3	*T. guilinensis* sp. nov.	GXNU YU000983	Tianhu Lake, Quanzhou County, Guilin City, Guangxi, China	PZ255435	PZ247723
4	*T. guilinensis* sp. nov.	GXNU YU000984	Tianhu Lake, Quanzhou County, Guilin City, Guangxi, China	PZ255436	PZ247724
5	*T. guilinensis* sp. nov.	GXNU QZXZ01	Tianhu Lake, Quanzhou County, Guilin City, Guangxi, China	PZ255432	PZ247720
6	*T. guilinensis* sp. nov.	GXNU YU001042	Tianhu Lake, Quanzhou County, Guilin City, Guangxi, China	PZ255437	PZ247725
7	*T. guilinensis* sp. nov.	GXNU YU001043	Tianhu Lake, Quanzhou County, Guilin City, Guangxi, China	PZ255438	PZ247726
8	*T. gaowangjienensis*	HNNU 20210425001	Gaowangjie National Nature Reserve, Hunan, China	PP090893	PP092977
9	*T. gaowangjienensis*	HNNU 20210508001	Gaowangjie National Nature Reserve, Hunan, China	PP090894	PP092978
10	*T. gaowangjienensis*	HNNU 20210504001	Gaowangjie National Nature Reserve, Hunan, China	PP090895	PP092979
11	*T. gaowangjienensis*	HNNU 20210504002	Gaowangjie National Nature Reserve, Hunan, China	PP090896	PP092980
12	*T. gaowangjienensis*	HNNU 20210508002	Gaowangjie National Nature Reserve, Hunan, China	PP090897	PP092981
13	*T. anhuiensis*	CIB08042905-2	Yuexi Co., Anhui, China	KY800587	KY800853
14	*T. anhuiensis*	CIB08042905-3	Yuexi Co., Anhui, China	KY800588	KY800854
15	*T. anhuiensis*	CIB08042905-4	Yuexi Co., Anhui, China	KY800589	KY800855
16	*T. broadoridgus*	CIB200085	Sangzhi Co., Hunan, China	KY800569	KC147814
17	*T. dabienicus*	HNNU1004-015	Shangcheng Co., Anhui, China	KY800607	KC147811
18	*T. dabienicus*	HNNU1004-024	Shangcheng Co., Anhui, China	KY800608	KC147812
19	*T. dabienicus*	HNNU1004-026	Shangcheng Co., Anhui, China	KY800609	KY800869
20	*T. daloushanensis*	CIBWG200600019	Suiyang Co., Guizhou, China	KY800544	KY800817
21	*T. daloushanensis*	CIBWG20060007	Suiyang Co., Guizhou, China	KY800545	KY800818
22	*T. hainanensis*	CIB20081048	Mt. Diaoluo, Hainan, China	KY800553	KC147817
23	*T. himalayanus*	CIB201406246	Mai Pokhari, Mechi, Nepal	KY800590	KT765173
24	*T. kachinorum*	ZMMU A5953	Ingyin Taung Mt, Kachin, Myanmar	MK095618	MK097273
25	*T. kweichowensis*	CIBWg200808 18014	Bijie City, Guizhou, China	KY800551	KY800823
26	*T. kweichowensis*	GZNU20180516035	Nayong Co., Guizhou, China	OM228750	OM164016
27	*T. liuyangensis*	CIB110601F06	Liuyang City, Hunan, China	KY800615	KY800875
28	*T. lizhenchangi*	KUHE:42316	Yizhang Co., Hunan, China	KY800621	KY800881
29	*T. maolanensis*	CIBWg20090730001	Libo Co., Guizhou, China	KY800575	KY800842
30	*T. maolanensis*	CIBML20180427001	Libo Co., Guizhou, China	MK835787	MK820699
31	*T. maolanensis*	CIBWg20090730004	Libo Co., Guizhou, China	KY800580	KY800846
32	*T. maolanensis*	CIBWg20090730005	Libo Co., Guizhou, China	KY800578	KY800845
33	*T. maolanensis*	CIBML20180427003	Libo Co., Guizhou, China	MK835789	MK820701
34	*T. pseudoverrucosus*	CIBWCG2012003	Ningnan Co., Sichuan, China	KY800597	KY800861
35	*T. pulcherrimus*	KUHE:46406	Pet Trade	KY800620	KY800880
36	*T. shanjing*	CIB980004	Baoshan City, Yunnan, China	KY800562	KY800831
37	*T. taliangensis*	CIBGG200110183	Shimian Co., Sichuan, China	KY800559	KC147819
38	*T. thaiorum*	ZMMU A-7577	PuHoatNR, NgheAn, Vietnam	MW883482	MW883478
39	*T. tongziensis*	CIB WB2020081511	Tongzi Co., Guizhou, China	OK338496	OK349411
40	*T. tongziensis*	CIB TZ20160714002	Tongzi Co., Guizhou, China	OK338498	OK349413
41	*T. tongziensis*	CIB WB2020202	Tongzi Co., Guizhou, China	OK338500	OK349415
42	*T. verrucosus*	CIB-TSHS1	Longchuan Co., Yunnan, China	KY800581	KY800847
43	*T. vietnamensis*	IEBRA.0701	Mauson, LangSon, Vietnam	KY800613	KY800873
44	*T. wenxianensis*	CIB 20070639	Qingchuan Co., Sichuan, China	KY800542	KY800815
45	*T. wenxianensis*	CIB20090527	Wenxian Co., Gansu, China	KY800579	KC147813
46	*T. wenxianensis*	CIB2010123101	Pingwu Co., Gansu, China	KY800604	KY800867
47	*T. wenxianensis*	CIB2010123102	Pingwu Co., Gansu, China	KY800605	KY800868
48	*T. yangi*	KUHE:42282	PetTrade	KY800624	KY800887
49	*T. ziegleri*	VNMN3390	QuanBa, HaGiang, Vietnam	KY800625	KY800889
50	*T. anguliceps*	NUOL 00420	/	/	KT304301
51	*T. ngarsuensis*	LSUHC13762	Shan State, Myanmar	/	MH836585
52	*T. notialis*	VNMNTA01229	Pu Hoat, Nghe An, Vietnam	/	HM462061
53	*T. panhai*	NUOL 00421	/	/	KT304310
54	*T. panwaensis*	CAS 245418	/	/	KT304279
55	*T. pasmansi*	IEBR:4466	/	/	MT210166
56	*T. phukhaensis*	CUMZ-A-7717	/	/	MN912573

No.	Species	Voucher number	Locality	GenBank accession no.	
				16S rRNA	ND2
57	*T. podichthys*	NCSM 77725	/	/	KT304295
58	*T. shanorum*	KUHE 42348	Shan State, Myanmar	/	AB769544
59	*T. sini*	SYS a008355	/	/	OK539837
60	*T. sparreboomi*	IEBR:4467	/	/	MT210167
61	*T. uyenoi*	KUHE:19147	Doi Suthep, Chiang Mai, Thailand	/	AB830733
62	*T. asperrimus*	CIB20070715	Jinxiu Co., Guangxi Province, China	KY800565	KY800834
63	*T. asperrimus*	CIBGX200807016	Jinxiu Co., Guangxi, China	KY800550	KY800822
64	*T. asperrimus*	CIBGX200807012	Jinxiu Co., Guangxi, China	KY800548	KY800821
65	*T. asperrimus*	CIBGX200807010	Jinxiu Co., Guangxi, China	KY800547	KY800820
66	*T. asperrimus*	CIBGX20080714	Jinxiu Co., Guangxi, China	KY800546	KY800819
67	*T. asperrimus*	CIB 200807055	Jinxiu Co., Guangxi, China	KY800566	KC147815
68	*T. asperrimus*	KIZ YPX9918	Mt. Dayaoshan, Guangxi, China	/	KT304303
69	*T. asperrimus*	YPX9919	Mt. Dayaoshan, Guangxi, China	/	JQ046345
70	*T. asperrimus*	YPX9920	Mt. Dayaoshan, Guangxi, China	/	JQ046347
71	*T. asperrimus*	YPX9922	Mt. Dayaoshan, Guangxi, China	/	JQ046346
72	*T. asperrimus*	YPX9923	Mt. Dayaoshan, Guangxi, China	/	JQ046348
73	*T. asperrimus*	CIB 70063	Longsheng, Guangxi, China	KY800549	KC147816
74	*T.* cf. *asperrimus* Baise	KIZ08080215	Baise, Guangxi, China	/	JQ046340
75	*T.* cf. *asperrimus* Baise	KIZ08080216	Baise, Guangxi, China	/	JQ046341
76	*T.* cf. *asperrimus* Baise	KIZ08080217	Baise, Guangxi, China	/	JQ046338
77	*T.* cf. *asperrimus* Baise	KIZ08080219	Baise, Guangxi, China	/	JQ046339
78	*T.* cf. *asperrimus* Guipin	SYS a006890	Guiping, Guangxi, China	/	OK539838
79	*T.* cf. *asperrimus* Guipin	SYS a006891	Guiping, Guangxi, China	/	OK539839
80	*T.* cf. *asperrimus* Guipin	SYS a008200	Guiping, Guangxi, China	/	OK539840
81	*T.* cf. *asperrimus* Guipin	SYS a008201	Guiping, Guangxi, China	/	OK539841
82	*T. wufengensis*	CIB WH10007	Wufeng Co., Hubei Prov., China	KY800603	KY800866
83	*T. wufengensis*	CIB WH10003	Wufeng Co., Hubei Prov., China	KY800602	KY800865
84	*T. koliaensis*	ZMMU A-8160	Kolia, Thanh Cong, Nguyen Binh, Cao Bang, Vietnam	PQ530965	PQ530362
85	*T. koliaensis*	ZMMU A-8157	Kolia, Thanh Cong, Nguyen Binh, Cao Bang, Vietnam	PQ530962	PQ530359
86	*E. chinhaiensis*	CIBZHJY2	Zhenhai Co., Zhejiang, China	KY800628	KY800892
87	*E. andersoni*	MVZ232187	/	/	EU880314

We conducted an analysis of species delimitation using the Assemble Species by Automatic Partitioning method (ASAP; Puillandre et al. 2021) and the simple distance model (*p*-distance). The partitioning with the lowest ASAP score was selected as optimal, following Puillandre et al. (2021).

Morphometric measurements

Morphometric data were obtained using a digital caliper to the nearest 0.1 mm. Morphological terminology followed Huang et al. (2024) and Lyu et al. (2021). Seventeen morphological characters were measured: total length (TOL); snout–vent length (SVL); head length (HDL); head width (HDW); snout length (SL); eye diameter (ED); tail length (TAL); tail height (TH); internasal distance (IND); hand length (HL); length of lower arm (LLA); third finger length (FIIIL); tibia length (TL); third toe length (TIIIL); thigh length (TLH); trunk length (TRL); and interorbital distance (IOD).

Multivariate principal component analysis (PCA) was conducted in SPSS v.25.0 (SPSS Inc.), based on the correlation matrix of size-standardized measurements (all measurements divided by TOL) of adult males. Scatter plots of the scores of the first two factors of PCA were used to examine the differentiation between the new species and its closest relatives revealed by phylogenetic analyses. Differences in quantitative characters of adult males between these three species were also evaluated with *t*-tests in SPSS. In these analyses, Levene's test was also performed for each character to test for equality of variances.

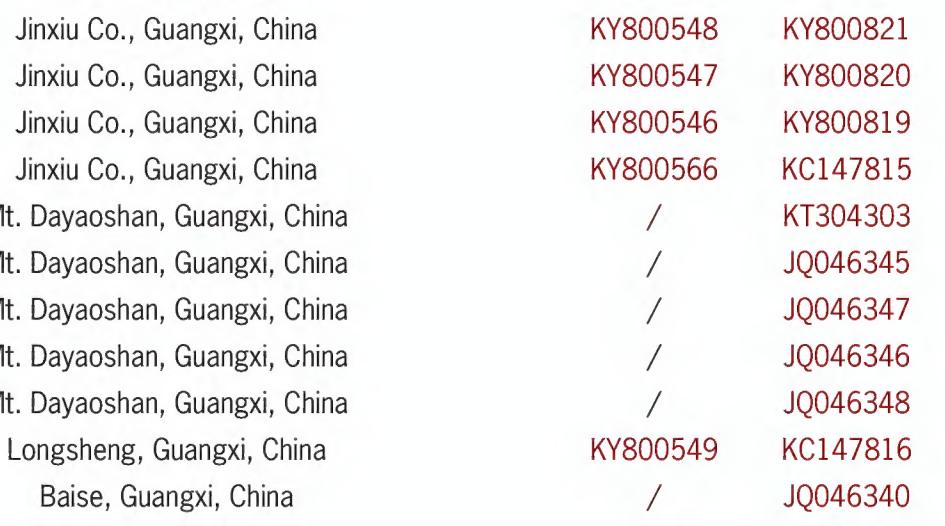

Figure 2. Scatterplot of principal components 1 and 2 of size-adjusted male morphometric data of *Tylototriton guilinensis* sp. nov., *T. gaowangjienensis*, and *T. dabienicus*.

Results

Phylogenetic relationship

The final alignments of 16S rRNA and ND2 sequences were 843 and 1041 bp, respectively, resulting in a concatenated sequence matrix of 1884 bp. Both maximum likelihood (ML) and Bayesian inference (BI) analyses yielded congruent topologies (Fig. 3). Phylogenetic reconstruction revealed three major clades within *Tylototriton*: Clade I (the *T. asperrimus* group), Clade II (the *T. verrucosus* group), and Clade III (the *T. taliangensis* group). Within Clade I, the specimens from Tianhu Lake, Quanzhou County, Guilin City, Guangxi Zhuang Autonomous Region, China, formed a highly supported novel lineage, and this lineage was resolved as sister to the clade of *T. gaowangjienensis* and *T. dabienicus* with strong support (Fig. 3). In addition, the samples from southwestern Guangxi (Baise), previously identified as *T. asperrimus* (Yuan et al. 2011), were grouped together with *T. sini* with strong support.

Under the Kimura 2-parameter model, genetic distances between the novel lineage and other *Tylototriton* species ranged from 1.47% (vs. *T. dabienicus*) to 14.01% (vs. *T. uyenoi*, Nishikawa, Khonsue, Pomchote & Matsui,

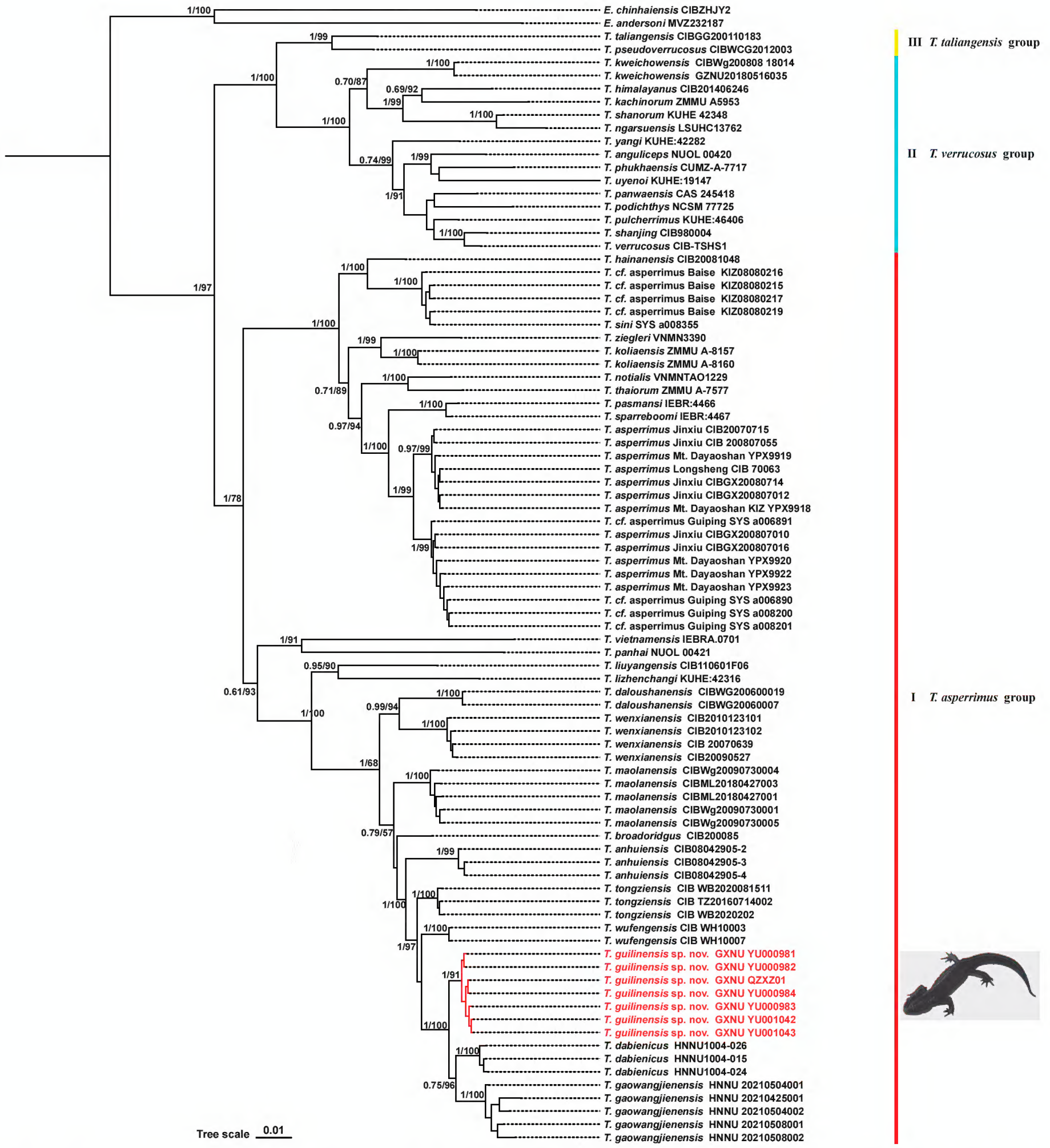

Figure 3. Bayesian phylogram of *Tylototriton* inferred from 16S rRNA and ND2 genes. Numbers above and below branches are Bayesian posterior probabilities and ML bootstrap values (only values above 50% are shown), respectively.

2013) in ND2 sequences (Suppl. material 1). The divergence between the unnamed lineage and its close relatives (*T. dabienicus* and *T. gaowangjienensis*) is 1.47%–1.63%, which is comparable to the divergences observed among recently described species (e.g., 1.17% between *T. pasmansi* and *T. sparreboomi*; 1.17% between *T. shanjing* and *T. verrucosus*; 1.71% between *T. gaowangjienensis* and *T. dabienicus*; and 1.79% between *T. shanorum* Nishikawa, Matsui & Rao, 2014 and *T. ngarsuensis* Phung, Pham, Nguyen, Ninh, Nguyen, Bernardes, Le, Ziegler & Nguyen, 2023).

The optimal partitioning scheme (score = 3.5) obtained by the ASAP analysis delineated *Tylototriton* samples included in this study into 38 operational taxonomic units (OTUs), one of which corresponds to the novel lineage comprising samples from Tianhu Lake (Fig. 4). With the exception of *T. sparreboomi* and *T. pasmansi*, which were grouped into a single OTU, all other OTUs corresponded to currently recognized species (Fig. 4).

Morphological study

Morphological data were summarized in Table 2. The *t*-tests revealed that male specimens from Guilin significantly ($p < 0.05$) differ from male types of *T. dabienicus* in HDL, HDW, TH, HL, TLH, and TOL (Table 3), and from male types of *T. gaowangjienensis* in HDL, HDW, TH, HL, TLH, and TOL (Table 4). The PCA analysis showed that the first two principal components accounted for 56.188% of the total variance (Table 5). Loadings for PC1, which account for 35.013% of the total variance, were most heavily loaded on SVL, HDW, TH, and HL. Loadings for PC2, which account for 21.175% of the total variance, were most heavily loaded on IND and IOD. Differentiation was found along the PC1 axis between the specimens from Guilin, *T. gaowangjienensis*, and *T. dabienicus* from the type locality (Fig. 2). This result indicates that specimens from Guilin differ from *T. dabienicus* and *T. gaowangjienensis* (e.g., shorter SVL, narrower HDW, lower TH, and shorter HL).

Table 2. Measurements (mm) of *Tylototriton guilinensis* sp. nov. (1–5), *T. gaowangjienensis* (6–10), and *T. dabienicus* (11–12). Data of *T. gaowangjienensis* and *T. dabienicus* were obtained from Huang et al. (2024).

ID	Voucher no.	Sex	TOL	SVL	HDL	HDW	SL	ED	TAL	TH	IND	HL	LLA	FIIIL	TL	TIIIL	TLH	TRL	IOD
1	GXNUYU000981	M	109.3	65.3	14.3	15.4	4.5	2.9	48.9	8.4	4.6	13.7	7.4	3.7	6.6	5.5	7.9	45.7	7.4
2	GXNUYU000982	M	108.1	59.7	12.5	12.8	3.8	2.9	53.8	7.3	3.8	12.3	5.7	3.5	6.1	4.1	6.9	42.3	6.3
3	GXNUYU000983	M	121.8	65.4	14.3	15.4	4.3	3.1	62.6	7.9	4.1	14.0	7.4	3.8	6.3	4.4	7.7	45.3	7.3
4	GXNUYU001042	M	131.0	67.8	15.9	16.5	5.1	3.0	72.2	7.9	4.5	13.7	7.8	3.0	6.2	5.5	7.9	46.3	7.9
5	GXNUYU001043	M	119.2	61.5	14.8	15.0	4.9	2.7	61.3	8.1	4.0	13.7	7.3	3.8	6.1	4.5	7.3	40.8	8.0
6	2021051701	M	123.7	67.2	15.9	14.1	4.4	3.8	56.1	7.0	4.3	8.5	8.7	3.9	6.6	5.9	7.1	40.4	7.9
7	2021051703	M	142.7	69.1	21.4	15.1	5.2	4.4	64.0	8.3	4.4	8.5	9.1	5.7	5.3	6.5	9.3	54.5	8.6
8	2021051704	M	136.3	71.1	17.4	15.6	5.4	4.2	64.6	8.3	5.9	8.0	6.6	3.9	5.8	5.4	6.8	48.0	8.7
9	HNNU 20210508002	M	129.3	59.8	20.3	13.9	5.5	8.4	69.5	7.3	5.9	4.2	6.9	5.0	6.8	5.7	5.8	43.6	8.3
10	HNNU 20210508003	M	129.3	62.1	19.1	14.5	6.0	3.6	67.2	7.0	6.7	6.6	6.8	4.1	7.9	5.0	7.0	46.2	8.6
11	CIB8042905	M	136.9	67.4	19.7	15.0	6.3	3.7	69.5	7.8	4.9	9.6	7.4	5.9	7.0	5.8	13.2	52.0	8.1
12	CIB80526010	M	158.9	74.0	20.9	15.5	5.9	4.0	74.9	8.1	5.0	9.8	7.0	5.4	7.5	5.0	12.1	57.3	7.6

Table 3. Summary statistics of male specimens (mean ± standard deviation) and results of the *t*-test between *Tylototriton guilinensis* sp. nov. ($n = 5$) and *T. dabienicus* ($n = 2$) from the type locality. The *t*-test was performed on the size-adjusted data, except TOL. * = $p < 0.05$.

Character	Mean ± SD	Mean ± SD	Levene's test		t-test	
	T. guilinensis sp. nov. ($n = 5$)	*T. dabienicus* ($n = 2$)	*F*	*p*-value	t	*p*-value
SVL	0.544 ± 0.0335	0.479 ± 0.0184	0.666	0.452	–2.508	0.054
HDL	0.122 ± 0.0060	0.138 ± 0.0085	0.372	0.569	2.896	0.034*
HDW	0.128 ± 0.0080	0.104 ± 0.0085	0.031	0.867	–3.497	0.017*
SL	0.038 ± 0.0028	0.042 ± 0.0064	7.916	0.037	0.664	0.614
ED	0.025 ± 0.0020	0.026 ± 0.0014	3.145	0.136	0.493	0.643
TAL	0.505 ± 0.0378	0.490 ± 0.0262	0.178	0.691	–0.505	0.635
TH	0.068 ± 0.0062	0.054 ± 0.0042	0.119	0.744	–2.778	0.039*
IND	0.036 ± 0.0036	0.034 ± 0.0035	0.001	0.973	–0.692	0.520
HL	0.115 ± 0.0071	0.066 ± 0.0057	0.004	0.954	–8.548	0.000*
LLA	0.061 ± 0.0053	0.049 ± 0.0071	0.356	0.577	–2.427	0.060
FIIIL	0.030 ± 0.0041	0.039 ± 0.0064	0.740	0.429	2.141	0.085
TL	0.054 ± 0.0055	0.049 ± 0.0028	1.485	0.277	–1.090	0.325
TIIIL	0.041 ± 0.0060	0.037 ± 0.0078	0.183	0.687	–0.841	0.439
TLH	0.064 ± 0.0047	0.086 ± 0.0141	8.513	0.033	2.152	0.260
TRL	0.375 ± 0.0302	0.371 ± 0.0134	1.453	0.282	–0.212	0.841
IOD	0.063 ± 0.0044	0.054 ± 0.0078	2.666	0.163	–2.106	0.089
TOL	117.858 ± 9.4609	147.900 ± 15.5563	1.080	0.346	3.278	0.022*

Table 4. Summary statistics of male specimens (mean ± standard deviation) and results of the *t*-test between *Tylototriton guilinensis* sp. nov. ($n = 5$) and *T. gaowangjienensis* ($n = 5$) from the type locality. The *t*-test was performed on the size-adjusted data, except TOL. * = $p < 0.05$.

Character	Mean ± SD	Mean ± SD	Levene's test		t-test	
	T. guilinensis sp. nov. ($n = 5$)	*T. gaowangjienensis* ($n = 5$)	*F*	*p*-value	t	*p*-value
SVL	0.544 ± 0.0335	0.498 ± 0.0332	0.074	0.792	–2.180	0.061
HDL	0.122 ± 0.0060	0.142 ± 0.0131	7.518	0.025	3.157	0.021*
HDW	0.128 ± 0.0080	0.111 ± 0.0041	0.533	0.486	–4.213	0.003*
SL	0.038 ± 0.0028	0.040 ± 0.0048	1.332	0.282	0.808	0.442
ED	0.025 ± 0.0020	0.037 ± 0.0156	4.924	0.057	1.706	0.126
TAL	0.505 ± 0.0378	0.487 ± 0.0402	0.385	0.552	–0.772	0.491
TH	0.068 ± 0.0062	0.057 ± 0.0026	1.257	0.295	–3.467	0.008*
IND	0.036 ± 0.0036	0.041 ± 0.0084	4.564	0.065	1.418	0.194
HL	0.115 ± 0.0071	0.054 ± 0.0140	1.876	0.208	–8.659	0.000*
LLA	0.061 ± 0.0053	0.058 ± 0.0090	3.674	0.092	–0.644	0.538
FIIIL	0.030 ± 0.0041	0.034 ± 0.0047	0.710	0.424	1.357	0.212
TL	0.054 ± 0.0055	0.049 ± 0.0096	2.529	0.150	–0.891	0.399
TIIIL	0.041 ± 0.0060	0.043 ± 0.0041	0.363	0.563	0.674	0.519
TLH	0.064 ± 0.0047	0.054 ± 0.0076	1.111	0.323	–2.388	0.044*
TRL	0.375 ± 0.0302	0.351 ± 0.0211	0.882	0.391	–1.471	0.180
IOD	0.063 ± 0.0044	0.064 ± 0.0022	6.353	0.036	0.361	0.731
TOL	117.858 ± 9.4609	132.252 ± 7.3490	0.354	0.568	2.687	0.028*

Therefore, integrating morphological and phylogenetic evidence, we consider that the Tianhu Lake population of *Tylototriton* represents a distinct new species and describe it herein.

Taxonomic account

Tylototriton guilinensis sp. nov.

https://zoobank.org/C3284BE7-488C-4CAC-88B1-48524B6ADBF4

Figs 5–7

Holotype. GXNU YU001042, adult male collected on 16 July 2025 by Wei Xiao and Xinbin Chen from Tianhu Lake, Quanzhou County, Guilin City, Guangxi Zhuang Autonomous Region, China (26°06'34.22"N, 110°53'56.69"E, 1789 m elevation).

Paratypes. Three adult males (GXNU YU000981, GXNU YU000982, and GXNU YU000983) and one adult female (GXNU YU000984) collected by Wei Xiao, Xiangjian Wu, Yuanqiang Pan, and Xinbin Chen on 10 May 2025 from the type locality; and one adult male (GXNU YU001043) collected on 16 July 2025 by Wei Xiao and Xinbin Chen from the type locality.

Etymology. The new species is named after its type locality, Guilin City in the Guangxi Zhuang Autonomous Region. We propose the Chinese name as "桂林疣螈" (Guì Lín Yóu Yuán) and the English common name as "Guilin Crocodile Newt."

Diagnosis. *Tylototriton guilinensis* sp. nov. can be distinguished from all other congeners by the following combination of morphological characteristics: (1) medium body size (117.9 ± 9.5 mm); (2) rib nodules flatten, indistinct, not separated, and almost in continuous longitudinal rows forming a dorsolateral fold; (3) orange coloration of the rib nodules absent; (4) orange markings on the parotoid absent; (5) head wider (HDW) than long (HDL) (HDL/HDW = 0.92–0.99); (6) finger tips extending beyond the snout when forelimbs stretched forward; (7) tips of forelimbs and hindlimbs reaching and overlapping when folded towards the body; (8) snout truncate, nearly square shaped in dorsal view; (9) gular fold present; (10) adult males possessing cloacal papillae within the fissure; (11) peripheral area of cloaca orange; and (12) the orange coloration at the ventral edge of tail contacted with the orange coloration around the cloaca.

Table 5. Factor loadings of the first two principal components of 16 size-adjusted male morphometric characteristics of *Tylototriton guilinensis* sp. nov., *T. gaowangjienensis*, and *T. dabienicus*. Absolute values of loading greater than 0.75 are in boldface. Abbreviations are defined in Materials and Methods.

Character	PC1	PC2
Eigenvalue	3.501	2.118
% variation	35.01%	21.18%
SVL	**0.949**	0.109
HDL	–0.717	0.471
HDW	**0.91**	0.304
SL	–0.365	0.601
ED	–0.530	0.540
TAL	–0.235	0.195
TH	**0.896**	0.197
IND	–0.222	**0.818**
HL	**0.921**	–0.213
LLA	0.632	0.272
FIIIL	–0.419	0.021
TL	0.333	0.485
TIIIL	0.325	0.582
TLH	0.122	–0.472
TRL	0.503	–0.110
IOD	0.361	**0.858**

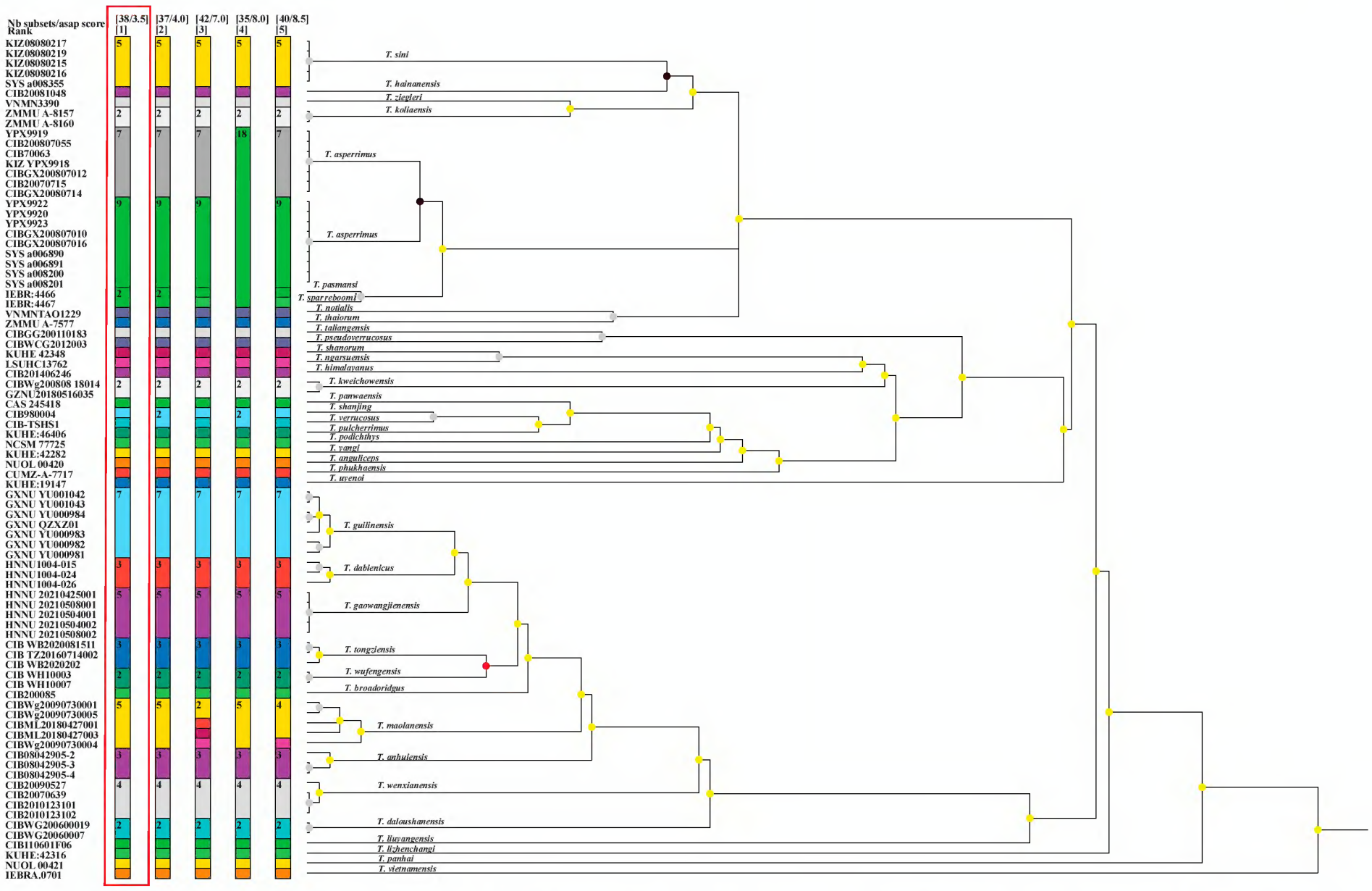

Figure 4. Species delimitation results obtained by ASAP based on ND2 sequences. Rank 1 represents the best partition, identifying 38 species within the genus *Tylototriton*.

Description of holotype. Adult male with medium size. Total length (TOL) 131.0 mm, snout-vent length (SVL) 67.8 mm, tail length (TAL) 72.2 mm; head wider than long (HDL/HDW = 0.96); snout truncate, nearly square-shaped in dorsal view, snout length exceeding eye diameter; projecting beyond lower jaw in lateral profile (Fig. 5); eyes relatively large (3.0 mm), laterally positioned but visible dorsally; eyelids nearly circular; gape straight, extending posteriorly beyond posterior eyelid margin; maxillary and premaxillary teeth present; vomerine teeth arranged in a continuous inverted V-shaped ridge between nostrils, extending to level of posterior orbital margin; tongue elliptical, attached anteriorly with free lateral margins; cranial ridges prominent, forming a nearly Π-shaped longitudinal ridge from snout tip to occiput with smooth margins; gular fold distinct; skin texture rough, densely covered with small granules on head dorsum, dorsal trunk, lateral flanks, and tail; dorsolateral warts flattened, inconspicuous, non-discrete, forming an almost continuous ridge; labial margins, digit tips, ventral surfaces of limbs, and ventral tail margin smooth. Limbs relatively slender; limb tips overlapping when adpressed to body; fingertips extending beyond snout when forelimbs adpressed anteriorly. Forelimbs with four fingers, relative length III > II > IV > I; hindlimbs with five toes, relative length III > IV > II > V > I; all digits slightly depressed, tips bluntly rounded, lacking webbing; tail height exceeding tail base width; dorsal tail fin thick and short; ventral tail fin slender, originating at tail base and not connecting to posterior margin of cloacal slit; cloacal region smooth; vent a longitudinal slit; distinctive orange pigmentation present on digit tips, pericloacal area, and ventral tail margin, forming a continuous stripe connecting cloacal and tail regions.

Coloration of holotype in life. Dorsal skin pale orange; ventral skin black; the parotoid gland region is pale orange; the ventrolateral edge of the tail, the extremities of the limbs, and the area surrounding the cloaca are orange-red (Fig. 5).

Coloration of holotype in preservative (75% ethanol). Dorsal skin black; ventral skin is tan; the parotoid gland region is black; the ventrolateral edge of the tail, the extremities of the limbs, and the area surrounding the cloaca are pale yellow (Fig. 6).

Secondary sexual characteristics. Adult males have papillae within the cloacal slit, whereas adult females exhibit a relatively smooth cloacal slit.

Morphological variation. Three paratypes (GXNU YU000983, GXNU YU000984, and GXNU YU001043) exhibit a vermilion spot on the palmar region at the base of the fourth finger (Fig. 7D–I). Paratype GXNU YU000983 exhibits a vermilion pigmentation on the dorsal tail tip (Fig. 7J). Four paratypes (GXNU YU000982, GXNU YU000983, GXNU YU000984, GXNU YU001043) possess horn-like projections on the parotoid glands (Fig. 7A–C).

Ecology, habitat, and distribution. *Tylototriton guilinensis* sp. nov. was discovered in a roadside pond and adjacent marsh wetlands at Tianhu Lake, Quanzhou County, Guangxi Zhuang Autonomous Region, China

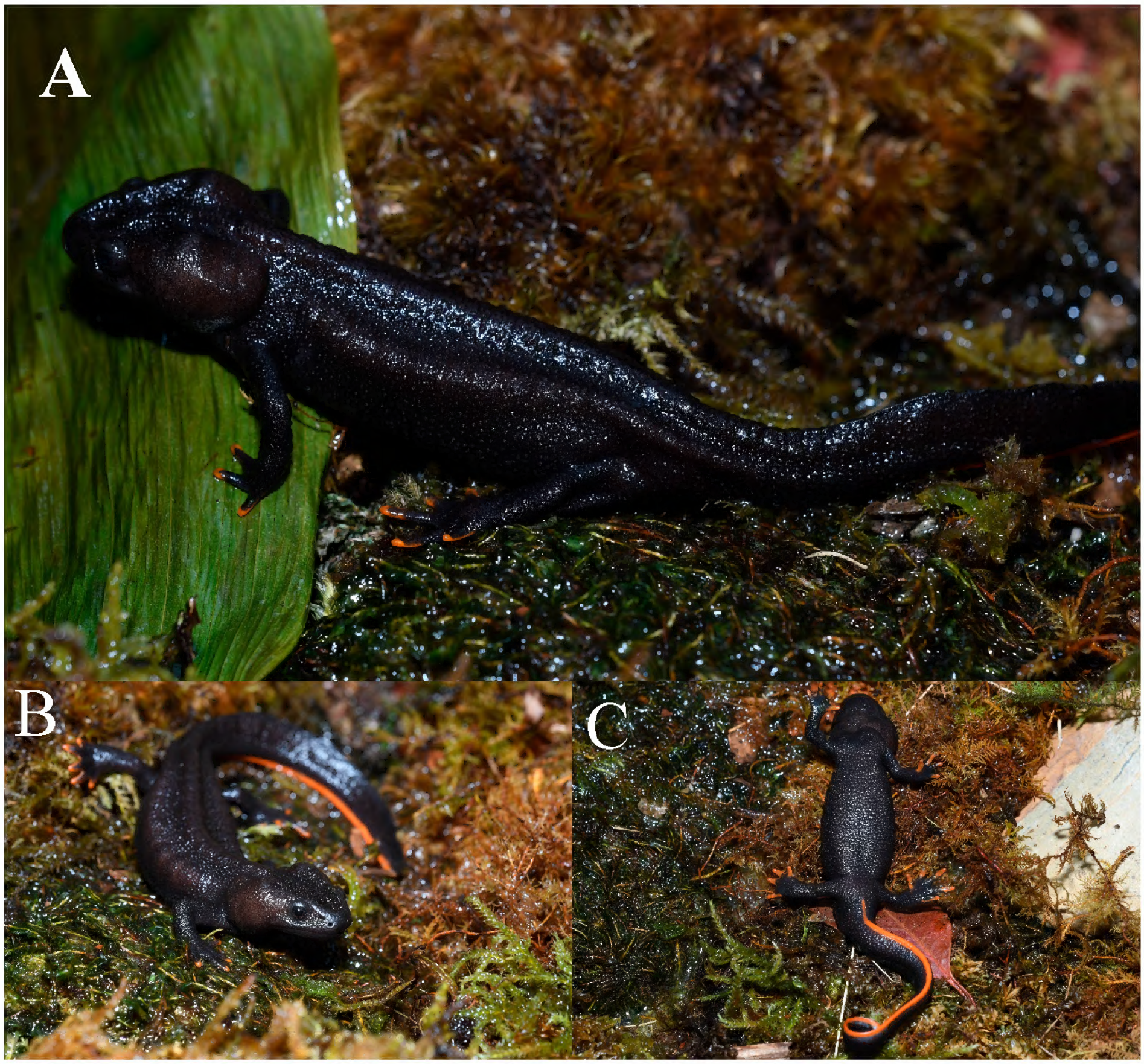

Figure 5. Dorsolateral (**A**), dorsal (**B**), and ventral (**C**) views of the holotype of *Tylototriton guilinensis* sp. nov. (GXNU YU001042) in life. (Photo by Yuanqiang Pan).

(Fig. 8). This species is currently known only from the type locality. During the survey in May 2025, coinciding with the breeding season, aggregations of individuals were observed in marshes and ponds after 19:30, though no eggs or larvae were detected. Sympatric species observed during the surveys include *Hynobius maoershanensis*, *Quasipaa boulengeri*, *Hoplobatrachus chinensis*, *Protobothrops jerdonii*, and *Azemiops feae*. The newt primarily inhabits evergreen broadleaf forests and marsh wetlands at elevations of 1,600–1,800 m. Breeding habitats are aquatic, comprising two types: ponds and marsh wetlands. Dominant vegetation in breeding areas consists of evergreen broadleaf canopy and wetland herbaceous plants. The microenvironment is characterized by dense canopy cover, high humidity, and a thick humus layer (Fig. 8).

Comparisons. The new species belongs to the *T. asperrimus* species group (Fig. 3). It can be distinguished from members of the *T. taliangensis* group (*T. taliangensis* and *T. pseudoverrucosus*) by body relatively robust, TAL/SVL < 120% in adult males (vs. body slender, TAL distinctly larger than SVL, TAL/SVL > 125% in adult males), and from members of the *T. verrucosus* group (*T. kweichowensis*, *T. himalayanus* Khatiwada, Wang, Ghimire, Vasudevan, Paudel & Jiang, 2015, *T. kachinorum* Zaw, Lay, Pawangkhanant, Gorin & Poyarkov, 2019, *T. shanorum*, *T. ngarsuensis*, *T. yangi*, *T. anguliceps* Le, Nguyen, Nishikawa, Nguyen, Pham, Matsui, Bernardes & Nguyen, 2015, *T. phukhaensis* Pomchote, Khonsue, Thammachoti, Hernandez, Peerachidacho, Suwannapoom, Onishi & Nishikawa, 2020, *T. uyenoi*, *T. panwaensis*, *T. podichthys* Phimmachak, Aowphol & Stuart, 2015, *T. pulcherrimus*, *T. shanjing*, *T. verrucosus*) by tail with different colorations, the ventral tail ridge with orange margin (vs. tail with uniform coloration, orange or light brown, much brighter and lighter than the ground coloration of body).

Figure 6. Views of the holotype of *Tylototriton guilinensis* sp. nov. (GXNU YU001042) in preservative. (Photo by Xiangjian Wu).

Within the *T. asperrimus* species group, the new species is closely related to *T. gaowangjienensis* and *T. dabienicus*. The new species can be distinguished from *T. gaowangjienensis* by head wider (HDW/TOL 0.128 ± 0.0080) than long (HDL/TOL 0.122 ± 0.0060) (vs. head longer [HDL/TOL 0.142 ± 0.0131] than wide [HDW/TOL 0.111 ± 0.0041]), longer SVL (SVL/TOL 0.544 ± 0.0335 vs. 0.498 ± 0.0332), wider HDW (HDW/TOL 0.128 ± 0.006 vs. 0.111 ± 0.0041), taller TH (0.068 ± 0.0062 vs. 0.057 ± 0.0026), and longer HL (0.115 ± 0.0071 vs. 0.054 ± 0.0140); from *T. dabienicus* by head wider (HDW/TOL 0.128 ± 0.008) than long (HDL/TOL 0.122 ± 0.0060) (vs. head longer [HDL/TOL 0.138 ± 0.0085] than wide [HDW/TOL 0.104 ± 0.0085]), finger tips extending beyond the snout when forelimbs stretched forward (vs. finger tips reaching the anterior corner of the eye), tips of forelimbs and hindlimbs overlapping when folded towards the body (vs. tips of fingers and toes do not meet or just meet when limbs are adpressed to the body), longer SVL (SVL/TOL 0.544 ± 0.0335 vs. 0.479 ± 0.0184), wider HDW (HDW/TOL 0.128 ± 0.0080 vs. 0.104 ± 0.0085), taller TH (0.068 ± 0.0062 vs. 0.054 ± 0.0042), and longer HL (0.115 ± 0.0071 vs. 0.066 ± 0.0057).

The new species differs from *T. asperrimus*, which was also recorded from northeastern Guangxi (Fig. 1), by rib nodules flatten, indistinct, not separated, and almost in continuous longitudinal rows forming a dorsolateral fold distinguishes (vs. rib nodules swollen, distinct, clearly separated or slightly contacted at the base) and finger tips extending beyond snout when forelimbs stretched forward (vs. reaching nostril).

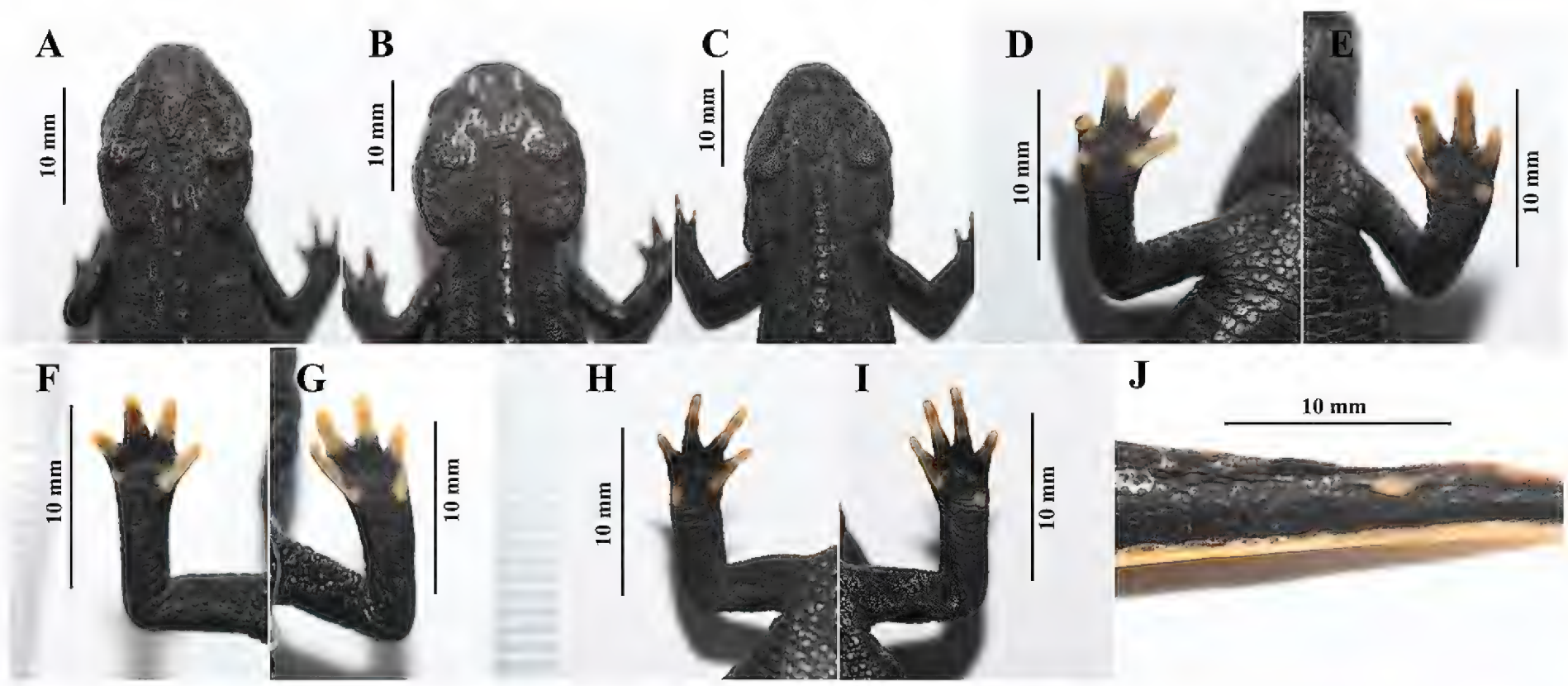

Figure 7. Morphology of parotoid glands (**A–C**), variation in pale yellow blotches on distal subarticular tubercles of digit IV (**D–I**), and coloration of dorsal tail tip (**J**) of *Tylototriton guilinensis* sp. nov. in preservative. GXNU YU000984: **A**, **F**, **G**; GXNU YU000983: **B**, **D**, **E**, **J**; GXNU YU001043: **C**, **H**, **I**. (Photo by Xiangjian Wu).

Figure 8. Habitat of *Tylototriton guilinensis* sp. nov. at the type locality. (Photo by Yuanqiang Pan).

The new species differs from *T. daloushanensis*, *T. sini*, *T. liuyangensis*, and *T. joe* by snout truncate, nearly square shaped in dorsal view (vs. bluntly rounded in *T. daloushanensis* and *T. liuyangensis*; nearly rounded hexagonal in dorsal view, depressed, gently sloping in profile in *T. sini*; and rounded in *T. joe*); from *T. anhuiensis*, *T. daloushanensis*, *T. koliaensis*, *T. maolanensis*, *T. lizhenchangi*, *T. sini*, *T. broadoridgus*, *T. liuyangensis*, *T. tongziensis* and *T. wenxianensis* by head wider than long (vs. longer than wide in *T. anhuiensis*, *T. daloushanensis*, *T. maolanensis*, *T. lizhenchangi*, and *T. sini*, head nearly as wide as long in *T. broadoridgus*, *T. koliaensis*, *T. liuyangensis* and *T. wenxianensis*); from *T. hainanensis*, *T. lizhenchangi*, *T. ziegleri*, and *T. joe* by rib nodules flatten, indistinct, not separated, and almost in continuous longitudinal rows forming a dorsolateral fold distinguishes (vs. rib nodules swollen, distinct, clearly separated or slightly contacted at the base); from *T. hainanensis*, *T. daloushanensis*, and *T. liuyangensis* by finger tips extending beyond snout when forelimbs stretched forward (vs. reaching eye in *T. hainanensis*, reaching the midpoint between eye and nostril in *T. daloushanensis*, reaching orbital region in *T. liuyangensis*, and reaching nostril in *T. asperrimus*); from *T. sini* and *T. ziegleri* by absence of orange coloration of the rib nodules (vs. rib nodules orange); from *T. wenxianensis* by peripheral area of cloaca orange (vs. peripheral area of cloaca brownish black); and from *T. wufengensis* by relative fingers length III > II > IV > I and relative toes length III > IV > II > V > I (vs. relative fingers length III > II > I > IV and relative toes length III > IV > II > I > V; Suppl. material 2).

Discussion

Emerging evidence indicates that species diversity of the genus *Tylototriton* has been severely underestimated (e.g., Lyu et al. 2021; Dufresnes and Hernandez 2022; Li et al. 2022; Luo et al. 2022; Rao 2022 "2020;" Decemson et al. 2023; Phung et al. 2023; Huang et al. 2024; Poyarkov et al. 2024; Li et al. 2026), and it has been documented that cryptic species of this genus may occur in Guangxi (Hernandez 2018), where only *T. asperrimus* is formally recognized (AmphibiaChina 2026). In this study, we confirm that the species diversity of *Tylototriton* was underestimated and raise the number of species to three in Guangxi. Firstly, based on molecular and morphological evidence, we describe a novel species from Quanzhou, northeastern Guangxi. Secondly, we find that the *Tylototriton* specimens from Baise, which were identified as *T. asperrimus* (Yuan et al. 2011), clustered with *T. sini*. Therefore, based on the

phylogenetic results of this study, we revise this population to *T. sini*. In addition, we find that *T. asperrimus* comprises two highly supported mitochondrial subclades that co-occur at the type locality (Mt. Dayao, Jinxiu, Guangxi; Fig. 3), and the genetic distance between them (1.27%) is comparable to the divergence between some *Tylototriton* species. Therefore, based on the above findings, we consider that more studies are required to unveil the species diversity of *Tylototriton* in Guangxi and to investigate the genetic structure of *T. asperrimus*. Considering the discontinuous distribution of *T. sini* in western Guangdong and western Guangxi (Fig. 1), probably more distribution records of this species would be discovered in Guangxi.

With the inclusion of *Tylototriton guilinensis* sp. nov., two *Tylototriton* species (along with *T. asperrimus*) currently occur in the northeastern part of Guangxi, a geographical region situated at the western end of the Nanling Mountains. In recent years, a number of new amphibian species have been identified in this region (e.g., Lyu et al. 2019; Chen et al. 2022; Luo et al. 2025; Wu et al. 2025a, 2025b). The Nanling Mountains are composed of a series of discontinuous mountains separated by basins, terraces, plains, and hills with low altitude (Miao et al. 2020). As a biodiversity hotspot, the Nanling Mountains have exceptional richness and endemism of amphibian species (Xu et al. 2024). Thus, more efforts should be made to better document and understand species diversity in this region.

Amphibians are currently the most threatened vertebrates (Cox et al. 2022). Studies have shown that habitat fragmentation and loss are important reasons for the decline in amphibian populations (Alford et al. 1999; Luedtke et al. 2023). Habitat fragmentation can lead to the isolation of continuous large populations, thereby forming isolated small populations, affecting the dispersal and gene flow between populations, and further resulting in the decline of population adaptability and genetic diversity (Hitchings et al. 1998). At present, *T. guilinensis* sp. nov. is only found in Tianhu Wetland Park in Quanzhou County, Guilin City, and its habitat is facing challenges due to human activities such as wind power development and road construction. Therefore, to better understand and protect this new species, it is imperative to conduct wide field surveys on its critical information (e.g., distribution range, population size, and other key biological and ecological traits), crack down on illegal capture, and reduce interference from human activities in its habitat.

A key to species within *Tylototriton asperrimus* group

1	Vertebral ridge segmented, tuberculate	*T. ziegleri*
–	Vertebral ridge not segmented	2
2	Rib nodules flatten, indistinct, not separated, and almost in continuous longitudinal rows forming a dorsolateral fold	3
–	Rib nodules swollen, distinct, clearly separated or slightly contacted at the base	9
3	Orange markings on the parotoid present in males	*T. lizhenchangi*
–	Orange markings on the parotoid absent in males	4
4	Head width larger than or equal to head length	5
–	Head longer than wide	6
5	Peripheral area of cloaca brownish black	*T. wenxianensis*
–	Peripheral area of cloaca orange	18
6	Relative toe lengths III > II > IV > I > V	22
–	Relative toe lengths III > II > IV > V > I	7
7	Vertebral ridge rather wide, its width approximately equal to the eye diameter	*T. broadoridgus*
–	Vertebral ridge narrow, its width smaller than the eye diameter	8
8	The orange coloration at the ventral edge of tail contacted with the orange coloration around the cloaca	21
–	The orange coloration at the ventral edge of tail isolated from the orange coloration around the cloaca	*T. dabienicus*
9	Orange markings on the parotoid present	10
–	Orange markings on the parotoid absent	11
10	Anterior half of head and vertebral ridge yellow to reddish brown	*T. panhai*
–	Anterior half of head and vertebral ridge dark brown, with the same color as the ground coloration of body	*T. notialis*
11	Head wider than long	12
–	Head longer than wide	13
12	Sagittal bony ridge on head strong	*T. asperrimus*
–	Sagittal bony ridge on head obscure	*T. hainanensis*
13	Orange coloration of the rib nodules present	14
–	Orange coloration of the rib nodules absent	15
14	Smaller body size with TOL 118.4–124.5 mm in adult males	*T. sini*
–	Larger body size with TOL 151.0–172.0 mm in adult males	*T. maolanensis*
15	Gular fold absent	*T. vietnamensis*
–	Gular fold present	16
16	Snout obtusely rounded in dorsal view; rib nodules light brown	*T. thaiorum*
–	Snout truncate in dorsal view; rib nodules uniformly black	17

17 Tips of fingers reaching nostril, rib nodules slightly enlarged round-like ..... *T. sparreboomi*
– Tips of fingers reaching eye, rib nodules slightly smaller, pointy to round..... *T. pasmansi*
18 Tips of forelimbs and hindlimbs overlapping when folded towards the body 19
– Tips of fingers and toes do not meet when folded towards the body..... *T. liuyangensis*
19 Head as wide as long..... *T. koliaensis*
– Head wider than long 20
20 Relative fingers length III > II > IV > I; and relative toes length III > IV > II > V > I..... *T. guilinensis*
– Relative fingers length III > II > I > IV, and relative toes length III > IV > II > I > V ..... *T. wufengensis*
21 Snout edge round..... *T. gaowangjienensis*
– Snout is nearly square..... *T. anhuiensis*
22 Snout edge round..... *T. daloushanensis*
– Snout is nearly square..... *T. tongziensis*

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Supplementary material 1

Genetic distances between members of *Tylototriton* (Kimura 2-parameter) in ND2 sequences

Authors: Wei Xiao
Data type: xls
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Link: https://doi.org/10.3897/zse.102.184792.suppl1

Supplementary material 2

Comparison of *Tylototriton guilinensis* sp. nov. with 16 species of the *T. asperrimus* group in China

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Data type: xls
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